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Nate G. McDowell[1], Craig D. Allen[2], Kristina Anderson-Teixeira[3,4], Brian H. Aukema[5], Ben Bond-Lamberty[6], Louise Chini[7], James S. Clark[8], Michael Dietze[9], Charlotte Grossiord[10], Adam Hanbury-Brown[11], George C. Hurtt[7], Robert B. Jackson[12], Daniel J. Johnson[13], Lara Kueppers[11,14], Jeremy W. Lichstein[15], Kiona Ogle[16], Ben Poulter[17], Thomas A.M. Pugh[18,19], Rupert Seidl[20,21] Monica G. Turner[22], Maria Uriarte[23], Anthony P. Walker[24], Chonggang Xu[25]

[1]Pacific Northwest National Laboratory, Richland, WA, 99354, USA

[2]US Geological Survey, Fort Collins Science Center, New Mexico Landscapes Field Station, Los Alamos, New Mexico, USA

[3]Conservation Ecology Center; Smithsonian Conservation Biology Institute; Front Royal, Virginia, USA

[4]Center for Tropical Forest Science-Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Republic of Panama

[5]Department of Entomology, University of Minnesota, St. Paul, MN 55108, USA

[6]Joint Global Change Research Institute, Pacific Northwest National Laboratory, 5825 University Research Ct. #3500, College Park, MD 20740, USA

[7]Department of Geographical Sciences, University of Maryland, College Park, MD 20742

[8]Nicholas School of the Environment, Duke University, Durham, NC 27708, USA

[9]Department of Earth and Environment, Boston University, Boston, MA 02215, USA

[10]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

[11]Energy and Resources Group, University of California, Berkeley, 310 Barrows Hall #3050, Berkeley, CA, 94720, USA

[12]Department of Earth System Science, Woods Institute for the Environment, and Precourt Institute for Energy, Stanford University, Stanford, CA 94305, USA

[13]School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611

[14]Division of Climate and Ecosystem Sciences, Lawrence Berkeley National Laboratory, 1 Cyclotron Road, Berkeley, CA 94720, USA

[15]Department of Biology, University of Florida, Gainesville, FL 32611, USA

[16]School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff, AZ 86001, USA

[17]NASA Goddard Space Flight Center, Biospheric Sciences Lab., Greenbelt, MD 20771, USA

[18]School of Geography, Earth and Environmental Sciences, University of Birmingham, B15 2TT Birmingham, United Kingdom;

[19]Birmingham Institute of Forest Research, University of Birmingham, B15 2TT Birmingham, United Kingdom;

[20]Department of Forest and Soil Sciences, University of Natural Resources and Life Sciences Vienna, Austria

[21]School of Life Sciences, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

[22]Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI 53706, USA

[23]Department of Ecology, Evolution & Environmental Biology, Columbia University, New York, NY 10027, USA

[24]Environmental Sciences Division and Climate Change Science Institute, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA

[25]Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM 87545, USA

Enhanced abstract.

Background: Forest dynamics arise from the interplay of chronic drivers and transient disturbances with the demographic processes of recruitment, growth, and mortality. The resulting trajectories of vegetation development drive the biomass and species composition of terrestrial ecosystems. Forest dynamics are changing due to anthropogenic-driven exacerbation of chronic drivers, such as rising temperature and CO_2, and increasing transient disturbances, including wildfire, drought, windthrow, biotic attack, and land-use change. There are widespread observations of increasing tree mortality due to changing climate and land use, accompanied by observations of growth stimulation of younger forests due to CO_2 fertilization. These antagonistic processes are co-occurring globally, leaving the fate of future forests uncertain. We examine the implications of changing forest demography and its drivers as a critical uncertainty for both future forest management and forecasting impacts of global climate forcing.

Advances: We reviewed the literature of forest demographic responses to chronic drivers and transient disturbances to generate hypotheses on future trajectories of these factors and their subsequent impacts on vegetation dynamics, with a focus on forested ecosystems. We complemented this review with analyses of global land-use change and disturbance datasets to independently evaluate the implications of changing drivers and disturbances on global-scale tree demographics. Ongoing changes in environmental drivers and disturbance regimes are consistently increasing mortality and forcing forests towards shorter and younger stands, reducing potential carbon storage. Acclimation, adaptation, and migration may partially mitigate these effects. These increased forest impacts are due to natural disturbances (e.g. wildfire, drought, windthrow, insect/pathogen outbreaks) and land-use change, both of which are predicted to increase in magnitude in the future. Tree growth, and potentially recruitment, may have increased globally in the 20th century based on atmospherically derived estimates of the terrestrial carbon sink and based on remote sensing data, but the growth of this carbon sink has slowed. Variability in growth stimulation due to CO_2 fertilization is evident globally, with observations and experiments suggesting that forests benefit from CO_2 primarily in early stages of secondary succession. Furthermore, increased tree growth typically requires sufficient water and nutrients to take advantage of rising CO_2. Collectively, the evidence reveals that it is highly likely that tree mortality rates will continue to increase while recruitment and growth will respond to changing drivers in a spatially and temporally variable manner. The net impact will be a reduction in forest canopy cover and biomass.

Outlook: Pervasive shifts in forest vegetation dynamics are already occurring and are likely to accelerate under future global changes, with consequences for biodiversity and climate forcing. This conclusion is robust with respect to the abundant literature evidence and our global assessment of historical demographic changes, but it also forms the basis for hypotheses regarding the patterns and processes underlying the shifts in forest dynamics. These hypotheses will be directly testable using emerging terrestrial and satellite-based observation networks. The existing evidence and new observations provide a critical test of Earth system models that continue to improve in their ability to simulate forest dynamics and resulting climate forcing.

Ultimately, forest managers and natural resource policies must confront the consequences of changing climate and disturbance regimes to ensure sustainable forests and accrue their associated benefits.

Abstract: Forest dynamics arise from the interplay of environmental drivers and disturbances with the demographic processes of recruitment, growth, and mortality, subsequently driving the biomass and species composition of terrestrial ecosystems. However, forest disturbances and subsequent recovery are shifting with global changes in climate and land use, altering forest dynamics. Ongoing changes in environmental drivers, land use, and disturbance regimes are forcing forests towards younger, shorter stands. Rising CO_2, acclimation, adaptation, and migration can influence these impacts. Recent developments in Earth system models support increasingly realistic simulations of vegetation dynamics. In parallel, emerging remote sensing datasets promise qualitatively new and more abundant data on the underlying processes and consequences for vegetation structure. When combined, these advances hold promise to improve the scientific understanding of changes in vegetation demographics and disturbances. Pervasive shifts in forest dynamics are already occurring and are likely to accelerate under future global changes, with consequences for climate forcing.

Introduction

The interplay of vegetation demography—recruitment, growth, and mortality—with environmental conditions and disturbances drives forest dynamics of biomass, function, and species composition (Figure 1; see Box 1 for definitions). In old-growth forests that approximate steady-state demographics, the recruitment, growth, and mortality of trees are approximately balanced; in contrast, rapid recruitment often follows widespread disturbance-induced mortality (1). Vegetation dynamics may now be changing because the environmental context in which plant demography and disturbances interact is shifting with anthropogenic change (Figure 1). The interaction between episodic forest disturbances such as wind-throw or wildfire, and chronically changing drivers such as rising temperature, vapor pressure deficit (*VPD*), and CO_2, together with land-use change (2), leads to both compounding and antagonistic impacts that alter demographic rates (3), with consequences for terrestrial biogeochemical cycles and climate (4,5). Understanding the drivers of vegetation dynamics is thus critical for accurate prediction of global terrestrial biogeochemistry under future conditions (6).

The impacts of global change on forest demographic rates may already be materializing. In mature ecosystems, tree mortality rates have doubled throughout much of the Americas and in Europe over the last four decades (7-9). Simultaneously, global carbon budgets indicate either a growing or constant terrestrial carbon sink (10-12), which implies increased or constant vegetation production rates (13,14). However, satellite evidence suggests that forests might be switching from a CO_2 fertilization dominated period to a *VPD* dominated period (15). Terrestrial greening indices indicate a shift from a CO_2-driven increase in greenness in the late 20th century to a *VPD*-driven decrease in the last decade (16). Thus, increasing mortality due to anthropogenic changes, along with potentially increasing or stable growth and recruitment due to

133 CO_2 fertilization (5), represent opposing processes that are co-occurring globally, leaving the fate
134 of future forests uncertain.

135 Beyond changing vegetation dynamics within "intact" or relatively undisturbed forests,
136 episodic disturbances are tending to be larger, more severe and, in some regions, more frequent
137 under global change(17-20). Similarly, the rates and types of land-use change (*LUC*) vary widely
138 (21) but have, on average, increased globally in the past few centuries (2,22,23). Thus, at the
139 global scale, disturbances and *LUC* have likely amplified tree mortality beyond that suggested by
140 the doubling of background mortality rates in undisturbed forests (7-9). Current understanding
141 of the net balance of tree losses (mortality) and gains (recruitment and growth) under a changing
142 environment characterized by more extreme drivers and disturbances is limited, preventing
143 prediction of whether recruitment and growth can balance increased mortality rates in the future.

144 To evaluate whether environmental changes and increasing disturbances are causing
145 globally widespread shifts in vegetation demography, we reviewed global observations of
146 recruitment, growth, and mortality of forests and woodlands. Our expert-derived compilation of
147 the state-of-the-art knowledge on vegetation dynamics, their drivers, and disturbances, allowed
148 us to address four questions: i) Is there evidence for shifts in demography over recent decades?
149 ii) What physiological and disturbance-mediated processes underlie these demographic shifts?
150 iii) What are the potential consequences of disturbance-mediated changes in demography for
151 climate forcing? iv) How can global predictions of future vegetation dynamics best be improved?

152 **Evidence for changing drivers and disturbances and their impact on demography.**

153 Determining the impacts of changing drivers on demography is difficult given the lack of
154 global observation platforms. However, evidence abounds from individual published studies on
155 the drivers and their impacts on plant communities, and new modeling and observational efforts

now enable a more complete picture of disturbances and forest demography (24-26). In this section, we first examine if there are global trends in stand ages and test the sensitivity of the stand-age distribution to changes in disturbance rate using global datasets on *LUC* (27) and non-*LUC* (25,28) disturbances. We subsequently draw upon the wealth of published studies on changes in forest demographics and their drivers to investigate the potential changes leading to global age-trends. Ultimately, the combination of our global estimates along with the large literature base allows us to generate testable hypotheses regarding trends and impacts of the drivers of forest demographics.

Is disturbance changing forest demography at the global scale?

We re-analysed the Land-use Harmonization (*LUHv2*) dataset (28) with respect to forest age, revealing that the area of young forest stands (here defined as <140 years old) resulting directly from *LUC* (conversion of forest to non-forest) or wood harvest (reduction of biomass and age but retained as forest) has increased from 4.8 million km^2 in 1900 to 12.5 million km^2 in 2015 (or from 11.3% to 33.6% of forest area; Figure 2A). The results were insensitive to assumptions regarding the link of disturbance likelihood to stand age (Figure 2A). These forest stand age distributions exhibit different trajectories in different regions. Tropical forests have progressively lost old-growth area due to *LUC* over the 20^{th} century (Figure 3a, black dashed line). Wood harvest has increased from a minor driver of tropical forest age distribution in 1900 to a major one in 2015 (difference between solid and dashed lines). The split between deforestation and shifting cultivation drivers is broadly consistent with a satellite-based analysis for the period 2001-2015 (29). Temperate and Mediterranean forest ages are strongly influenced by wood harvest, which has made old-growth forests increasingly scarce in these regions. Boreal

179 forests saw little influence of *LUC* on stand age, but wood harvest has substantially shifted the
180 age distribution towards young forests.

181 In reality, old-growth forest are scarcer than that due to *LUC* and wood harvest (Figures
182 2a and 3), due to other disturbances that have shifted landscapes from old- to young-dominated
183 stands (14), such as wildfire (29), windthrows (30), and biotic outbreaks (31). To address these
184 additional disturbances, we integrated recent observation-based estimates of non-*LUC*
185 disturbance for closed-canopy forests (25,28) with *LUC* from *LUHv2*, to obtain a first principles
186 estimate of the combined effect of human and natural disturbances on forest age structure (Figure
187 2B). A twofold increase in non-*LUC* disturbance rates over the period 2015-2050 would result in
188 a substantial increase in the fraction of young forests (Figure 2B, C). Thus, realistic shifts in
189 disturbance rates can have substantial impacts on the age structure of forests in the future. As
190 discussed below, such an increase in disturbance rate is consistent with the magnitude of changes
191 observed or predicted in individual ecosystems.

192 Notably, calculations based on the Global Forest Age Dataset (GFAD) v1.1 (14,32)
193 yielded 16.5 M km2 old-growth and 26.3 M km2 of young forest (32), which differs from that in
194 Figure (2B, C). This disparity is likely attributable to consideration of different forest types
195 (closed-canopy versus all forests) and to differences in definition of stand size and age used in
196 inventories versus used in satellite-based estimates

197 ***Chronically changing drivers: Atmospheric CO_2*** has risen more than 125 ppm since the
198 industrial revolution (11), and is projected to rise an additional 50 to 200 ppm by 2100. Higher
199 CO_2 increases leaf-level water use efficiency, and rising CO_2 has positive but uncertain
200 feedbacks on plant demographic rates (Figure 4A-B). Maturation and seed production can be
201 accelerated under elevated CO_2 (33); however, seedling growth is not always stimulated by CO_2

(34). Recruitment response to rising CO_2 is variable (35,36). Forest inventory and tree-ring studies show limited evidence for CO_2 fertilization of growth (37-43), potentially due to the overwhelming influence of increasing drought and nutrient limitations (44). Ecosystem-scale CO_2 enrichment experiments in young forests suggest a 30% gain in decadal biomass increment (45), but experiments in mature forests have found minimal growth stimulation (46,47). This is consistent with evidence for an initially strong CO_2-related growth stimulation in young forests that decreases with tree age and size[39] due perhaps to nutrient (7,48) and hydraulic path-length limitations (49).

Limited studies suggest elevated CO_2 causes increased mortality or no change in mortality. Mortality rates of saplings during experimental drought were not mitigated by elevated CO_2 (50,51) while accelerated self-thinning due to CO_2 fertilization-induced stand density increases may lead to higher mortality (6,52,53) (Figure 4B). The latter process would be consistent with increases in recruitment at large scales. Because tree mortality is dominated by large size classes i.e. (54) (for details see section on size-related mortality below) faster growth via CO_2 fertilization may expose trees to size-related mortality risks earlier (7). Such CO_2-induced increases in mortality may be global (55). Furthermore, faster growth is often associated with lower wood density (56), rendering fast growing trees more susceptible to high winds. Thus, future CO_2 fertilization could increase recruitment, growth, and mortality (Figure 4B), though there is significant uncertainty about these effects.

Chronically changing drivers: Temperature and vapor pressure deficit are rising globally and will continue to rise into the future (57). Both temperature and *VPD* can have impacts on demographic rates. Rising temperature forces an exponential rise in *VPD*, which prompts

stomatal closure and limits photosynthesis, leading to lower growth, higher mortality (58), and reduced regeneration (59), and ultimately driving community shifts (60,61). These observations are consistent with hydraulic theory, which suggests that as *VPD* rises, potential maximum tree height declines (62) (Figure 5). This results from the dependency of water transport limitations on tree size (49) that are exacerbated by elevated *VPD* (Figure 5), making short stature advantageous with rising *VPD*. Because most plants cannot reduce their size (beyond limited reductions in leaf area or crown dieback), forests respond through increased mortality of large plants, which are replaced by smaller ones (62), as has been observed in many studies (26,54). While rising air temperature may also increase respiratory carbon loss, leaving less carbon for growth (63), warming in wetter and cooler regions may actually stimulate reproductive output, recruitment, and growth (64-66). Changes in temperature and *VPD* also can produce asynchrony in floral and pollinator phenology (67) and can reduce cold stratification (68), both of which reduce seed abundance (69), and negatively affect recruitment (70,71). Sapling mortality is accelerated by elevated temperature (71,72), but recruitment has increased in moist areas (73). Thus, rising temperature and *VPD* may be beneficial in cooler or wetter areas, but most evidence suggests negative impacts on plant demographic rates (Figure 4C, D; Figure 5).

Changing disturbance regimes: Droughts are anticipated to increase in frequency, duration, and severity globally (Figure 4E-F) and are more stressful to plants due to increases in temperature, *VPD*, and associated water loss (57). Drought can directly cause tree death or indirectly lead to mortality through associated increases in insect or pathogen attack (51). Hydraulic failure and carbon starvation remain the most likely, mutually inclusive, underlying physiological mechanisms for drought-induced mortality (74) and both processes are likely to increase tree susceptibility to biotic agents (75). Evidence suggests that drought-induced

mortality occurs more rapidly under warmer conditions (51.72). Consistent with these empirical results, models suggest far greater mortality of temperate conifer trees in the future (76). Reproductive output is often reduced by drought (but see (64)), which combined with drought impacts on seedling survival, leads to reduced recruitment (77). However, growth was relatively stable across a drought in Amazonia (78), while mortality increased. Thus, like rising temperature and *VPD*, it appears that drought may increase mortality regardless of location, while having variable impacts on recruitment and growth (Figure 4F).

Changing disturbance regimes: Land-use change and forest management have reduced vegetation stature and biomass, and altered species composition, with profound consequences for forest dynamics (Figures 2A, 4G-H). Today's global vegetation biomass stocks may amount to only ~50% of their potential due to *LUC* (79). Wood harvest and shifting cultivation are the land-use activities primarily responsible for the conversion from primary to secondary vegetation cover and associated demographic shifts (2). For systems that return to wild-vegetation or to managed forest after human clearing, demographic rates are typically accelerated. The increased resource availability after forest removal facilitates establishment of early-successional species, reduces species diversity (80,81), and causes a transition to younger, smaller plants (82). Post-deforestation recruitment is often prolific even in the absence of management (83). Globally, the recovery of harvested forests and abandoned agricultural land, along with establishment of new plantations, has resulted in younger forests (Figure 2A), with associated reductions in tree size and biomass (84). Such post-deforestation recruitment may be limited by elevated *VPD* or drought, as is the case with recruitment following all natural disturbances. Overall the net effect

of historical *LUC* and wood harvest has resulted in a substantial loss of forest area, along with altered demographic rates, leading to younger, shorter, less diverse ecosystems (Figure 4H).

Changing disturbance regimes: Wildfire is increasing in many forests worldwide (85) (Figure 4I), although human management of landscapes has led to wildfire suppression in some biomes (86). Given sufficient fuel, burned area increases exponentially with aridity (87), and future fire frequencies may exceed those documented over the past 10,000 years (88). Increased fire activity causes increased mortality and potentially higher recruitment and growth of either pre-existing or new species, but rates of recruitment and growth may be slowed under climate warming. Forests characterized by stand-replacing fire regimes are dominated by obligate seeders, and typically have effective seedling recruitment (89). However, high-severity and high-frequency fires can reduce recruitment by reducing seed supply through the repeated and severe loss of reproductively mature vegetation (90), and high frequency fires can cause recruitment losses via direct mortality of the seedbank, seedlings, and saplings (91), which is worsened by elevated *VPD* (92). Woody species that can resprout following fire, including shrubs that suppress tree regeneration (92), may be favored by increased fire frequency and severity. Increased fire severity results in high tree mortality in forests historically adapted to low-severity fires, and subsequent recruitment and growth may be slow or absent, resulting in conversion of forests to low-biomass ecosystems (93). Thus, wildfire can result in higher demographic rates, though rising temperature and *VPD* can negatively impact recruitment and growth (Figure 4J).

Changing disturbance regimes: Wind throw from cyclonic storms represents the dominant natural disturbance in coastal forests across the globe (94). Cyclonic storms are expected to

increase in frequency, wind velocities, and precipitation intensity (95) (Figure 4K), with more extreme flooding that promotes tree instability. Wind throw also results from convective thunderstorms and topographically mediated winds, and warming is expected to increase the frequency of atmospheric conditions conducive to severe thunderstorms (96). Canopy damage and whole-tree mortality are the most immediate impacts of wind throw (97) (Figure 4L). Larger trees dominate mortality from storms (98), and the loss of large canopy trees during wind disturbance favors growth of surviving trees (98,99) and advances regeneration, recruitment of early successional species (100), or resprouting of trees broken by wind (101). Depending on the resprouting or seeding capacity of surviving species, wind damage may slow or accelerate succession (102). We note that storms may also be associated with lightning, which may be a significant cause of large-tree mortality (103). Thus, windstorms should result in changes in all three demographic rates, though with large uncertainty at the global scale (Figure 4L).

Changing disturbance regimes: Biotic agents Biotic disturbances from insects, insect-pathogen complexes, and other biotic agents have been increasing in frequency, severity, and extent in recent decades (17,104,105) (Figure 3M). Such trends reflect a changing climate (106), altered land use (107), and introductions of non-indigenous insects and pathogens (108). Climate change is expected to further amplify biotic disturbances (109) in part through enhanced host vulnerability (Figure 4M). However, shifts in frequency or dampening of disturbance regimes could also emerge (110), leading to some uncertainty in outbreak dynamics under future conditions (Figure 4M). While insects and associated pathogens are globally widespread, lianas, or vines that use other plants as host structures, are increasing in abundance and are thought to be causing increasing mortality in the tropics (7,111).

317 Response of insects and pathogens to climate change is likely to increase plant mortality
318 (4), with variable impacts on growth and recruitment (Figure 4N). Tree mortality can result from
319 girdling of the phloem and xylem by bark beetles (75) and from repeated defoliation events that
320 exhaust the capacity of trees to recover (112). Tree mortality during outbreaks is usually partial
321 at the stand-level because many biotic agents preferentially attack trees of specific size- or
322 health-classes, or are host-specific (16). Suppressed, smaller trees and non-host tree species may
323 survive and grow rapidly when released from competition for resources (113,114). Thus, similar
324 to many other disturbances, mortality increases while recruitment and growth show variable
325 responses to biotic disturbances, including a dependency on post-disturbance temperature, *VPD*,
326 and drought.
327
328 ***On size and age demographics***. The combination of *LUC*, disturbances, and chronic drivers is
329 likely to have already shifted forests to younger and shorter stands, with these impacts increasing
330 under expected future changes in drivers and disturbances (Figure 2A-C). These results are
331 consistent with our review of the literature (Figure 4). Large trees are the most susceptible to die
332 from *LUC*-caused forest fragmentation (115,116), drought (26), rising temperature or *VPD*
333 (54,62) (Figure 5), windthrow (117,118), biotic attacks (119), and lightning (103), with variable
334 size-impacts of fire (120). The abundance of size-dependent mortality drivers and disturbances
335 should logically push stands towards younger/smaller distributions of trees and shorter statured
336 species assemblages (121).
337 There are exceptions to the pattern of climate drivers and disturbances reducing tree
338 height and stand age. Non-stand-replacing fires that kill smaller trees and leave the larger, older
339 trees will shift forests towards larger size distributions. Similarly, on occasions when droughts

preferentially kill younger but fast-growing trees, this would impact the subsequent size distribution and rate of carbon accumulation. Rising CO_2 and increased precipitation in some areas also counter the general decrease in size because they may lead to faster growth and hence taller trees (122). Thus, the antagonistic drivers promoting larger trees (e.g. rising CO_2) vs smaller trees (e.g. rising *VPD*, increasing disturbances) co-occur, but the general pattern of decreasing size and younger ages reveals that processes driving down size and age (Figures 2-5) are dominant globally.

Mitigation of demographic-disturbance impacts

The literature patterns suggest most drivers and disturbances will increase tree mortality now and in the future, with variable effects on recruitment and growth (Figure 4). The uncertainty grows, however, when we consider multiple feedbacks that can mitigate the changes in forest demography induced by chronically changing drivers and disturbance regimes. These processes include acclimation, adaptation, migration, and compensatory mechanisms of resource use. With global change, forests will be influenced by a combination of phenotypic plasticity (i.e. acclimation (123)), adaptation to novel biotic and abiotic stresses (124), and the ability to migrate as conditions change (125). Failure to acclimate, adapt, or migrate, including due to human infrastructure (126), could lead to recruitment and growth reductions and local extinctions. Plants have demonstrated acclimation of phenology, seed longevity, and metabolic processes to single and/or multiple stressors (127-130). Acclimation and adaptation will likely depend on an array of factors including genetic variation, fecundity, dispersal, population size, and environmental variability (123). Many tree species have migrated in response to past climatic cycles but at rates slower than the current pace of climate change (131). Regarding

resource use, reductions in stand density as a result of increased mortality or reduced recruitment should allow greater resource availability to surviving individuals, and therefore subsequently higher growth and survival rates (132). Such stand-resource mechanisms can manifest at the landscape scale, as most disturbances are patchy (133), and the size, shape, and arrangement of surviving forest patches can play a key role in recovery of the disturbed landscape (20). Taken together, the mitigating factors can play a significant role in buffering the impacts of changing drivers on plant survival, but it remains unclear if these factors will enable trees to keep pace with ongoing climate change (50,123). Ultimately, the uncertainty around future demographic rates shown in Figure 3 is partially because of the influence of these mitigating factors.

Consequences for community assembly and for climate forcing

The widespread shift in vegetation dynamics begets questions regarding consequences for community assembly and climate forcing. Hydraulic theory suggests that under rising *VPD,* functional traits of high conductance, low stature, and low leaf area should best enable survival, all of which are characteristics of pioneer, shrub and weed species (62). Consistent with this, diversity (e.g. species richness) temporarily increases post-disturbance for many systems, as short-statured, opportunistic species invade (134). If forest communities shift towards trait assemblages better suited to the new disturbance regime, such shifts may confer some resistance to future disturbances (134,135). Alternatively, if disturbance regimes shift faster than recruitment, growth, and subsequent community assembly can respond, resistance to future disturbances will likely decline.

Climate forcing responds to changing vegetation dynamics in complex ways. Changes in forest disturbance regimes and vegetation dynamics can affect climate via biogeochemical,

388 hydrological, and land-surface energy budgets (136). Reductions in biomass result in a loss of
389 carbon to the atmosphere despite younger, shorter stands often having higher gross
390 photosynthesis; this is due to the loss of carbon through decomposition of necromass, which is a
391 particularly large flux from mortality of older, larger trees such as those in old-growth forests
392 (137), and reduced landscape-mean carbon storage under an intensified disturbance regime
393 (138). The time required to re-achieve the same live carbon storage of an ecosystem after
394 disturbance can be decades to centuries, particularly if the disturbance cycle is increased, thus the
395 net effect of the biomass loss is increased CO_2 to the atmosphere and hence greater climate
396 forcing. This impact may be mitigated by increased carbon uptake due to CO_2 fertilization (139)
397 or enhanced recruitment. Calculations of the terrestrial carbon sink from atmospheric inversions
398 indicate that the sink grew over recent decades[12] due in part to increased leaf area (13),
399 consistent with increased recruitment and growth. However, evidence suggests that forests are
400 switching from a CO_2 fertilization dominated period to a *VPD* dominated period (15,16), despite
401 sustained high gross photosynthesis at the global scale (140). The increased mortality
402 throughout much of the terrestrial biosphere (7-9) further minimizes potential carbon storage
403 through the enhanced biomass loss. Ultimately, the terrestrial contribution to climate forcing
404 through carbon uptake and release results from the antagonistic process of rising CO_2 and forest
405 recovery from *LUC*, which enhance the carbon sink, and rising *VPD* and disturbances that reduce
406 the carbon sink.

407 Changing vegetation dynamics also influence regional and global surface energy budgets
408 and hydrological cycles. Disturbances frequently shift albedo of ecosystems from darker to
409 lighter, resulting in a decline in radiative forcing through less light absorption (141). The rate of
410 recruitment post disturbance influences the temporal period of this negative feedback (142). The

411 impact of changing vegetation dynamics on the water cycle is particularly complex. Evaporation
412 from canopies shifts as stands become taller because taller trees transpire less (per unit leaf area)
413 than smaller trees (49), but larger trees often have better rooting access to water sources and have
414 greater total leaf area. The net effect of disturbance is a transient decrease in evaporative loading
415 to the atmosphere along with albedo shifts, causing a feedback of decreasing precipitation
416 downwind (143,144). Ultimately, carbon storage is at least transiently reduced by disturbances,
417 with mixed impacts on the water and energy budgets.
418
419 **The path to improved prediction**

420 Changes in the global drivers of temperature, CO_2, *VPD*, and disturbances including
421 *LUC*, drought, wildfire, windstorms, and insect outbreaks, should all force forests towards
422 shorter, younger, lower biomass ecosystems. This trend is supported by hydraulic theory (62)
423 (Figure 5) and by abundant empirical evidence demonstrating a consistent increase in mortality
424 across the global-spectrum of drivers and disturbances and variable but often declining
425 recruitment and growth (Figure 4). While the bulk of evidence points to reduced plant stature
426 due to changing drivers, large uncertainty remains in the magnitude and slope of demographic
427 trajectories in the future (Figure 4). Given these trajectories, and the large uncertainties around
428 them, what are the critical next steps to allow improved global prediction? Continued long-term
429 observations (ground and remotely sensed) are essential to reveal the patterns of demographic
430 responses to drivers and disturbances; likewise, manipulative experiments are needed that alter
431 conditions such as CO_2 or drought to provide cause-and-effect understanding of the interactions
432 among mechanisms of demographic responses. However, for global-scale prediction of

responses and climate consequences we need to mainstream insights from observations and experiments into Earth system models (*ESM*s).

ESMs simulate the exchange of fluxes between the atmosphere, land, and ocean and stores of carbon, water, and energy; the land-surface modules of *ESMs* simulate the vegetation. *ESM*s have made great progress in simulating land use, disturbances, and demography, including representation of wildfire (145), drought-induced mortality (146), and cohort-age structured models that enable representation of succession and associated shifts in physiological traits (6). The global Coupled Model Intercomparison Projet CMIP6 now includes a dedicated model intercomparison activity focused on the effects of changes of land-use on carbon and climate (147). Advances in remote sensing and forest inventory integration are enhancing global datasets of forest structure (148) and age (32) that can be used in model initialization, data assimilation benchmarking, and sensitivity analyses (Figure 2A-C). These advancements set the stage for developments in *ESMs* such as the prediction of disturbances and demographic rate responses under climate and *LUC* scenarios.

The newest generation of *ESMs* utilize size or age-structured approaches to explicitly model demography in the Earth system (6), which should ultimately enable model-based representation of observed shifts in age structure (e.g. Figure 2). However, representation of vegetation demographic rates remains relatively simplistic. Simulation of growth responses to global change requires model refinement in light capture, belowground water and nutrient acquisition, and responses of respiration to temperature (6). Recruitment, including reproduction and dispersal, is the most undeveloped demographic process in *ESM* simulations. Reproductive allocation is invariant with plant functional type (*PFT*), and seed is assumed to mix evenly throughout a grid cell (but see (149)). Environmental constraints to *PFT* establishment are

456 derived from prior distributions of major taxa, and while recruitment rates can be influenced by
457 light or space availability, they are not responsive to temperature, CO_2, or soil moisture
458 (150,151). Simplistic dispersal assumptions are typically either overly permissive or restrictive.
459 Improvements in representing recruitment under global change are critical for improving
460 predictions of vegetation dynamics. These advancements will require data synthesis and new
461 data collection to support *PFT*-specific, environmentally sensitive parameterizations of
462 regeneration processes, such as reproductive allocation; effective dispersal; seedling
463 establishment, survival and growth; and post-disturbance recovery strategies (e.g., serotiny and
464 resprouting).

465 Disturbance-induced mortality is better developed for landscape-scale models than for
466 *ESM*s. *ESM* modeling of disturbance-induced mortality exists for wildfire and drought
467 (145,146), although significant challenges remain to represent both reliably globally, while *ESM*s
468 are under-developed for wind and insect mortality. Currently only one *ESM* to our knowledge
469 represents canopy damage (152); this causes *ESM*s to potentially underestimate the impacts of
470 drought and wind, as both disturbances cause lagged tree mortality associated with canopy loss
471 years after the inciting event (153,154). For insects, there have been prescriptive studies
472 examining the impact of insect outbreaks on land processes within *ESMs*, but no *ESM* has yet
473 explicitly considered the interaction between plant defense and insect population dynamics for
474 prediction of large-scale insect-induced tree mortality. For predicting wildfire, models should be
475 sensitive to both fuels and climate interactions and represent spatial patterns of burn severity
476 because the burn mosaic strongly influences postfire vegetation dynamics (145). Next-
477 generation demographic models are evolving to include explicit, mechanistic representations of
478 drought-associated mortality, including carbon starvation and hydraulic failure (155). The

evaluation of new hydraulics models (155) for prediction of mortality is an essential next step. Ultimately, model formulations that include environmentally sensitive, *PFT*-specific processes compatible with the cohort-based approach are likely to provide the best compromise between process-detail and parsimony and therefore most likely to capture changes in large-scale forest dynamics under future conditions.

Summary Forest vegetation dynamics (Figure 1) are already strongly influenced by global change (Figure 2) and will continue to be affected in the future (Figures 2-5) by changes in land use, chronic drivers such as CO_2 and *VPD*, and increasing frequency and severity of transient disturbances such as windthrow, wildfire, and insect outbreaks. Effects on forests are driven largely by consistent increases in tree mortality from these drivers, and variable responses of recruitment and growth depending on stand-age, disturbance type, and geographic location (Figure 4). The consequences of changing demographics suggest an increasing constraint in terrestrial carbon storage due, at least, to the consistent increase in mortality. Any declines in recruitment or growth, especially when disturbance-recovery cycles are disrupted, will exacerbate this carbon-cycle constraint. Shifts in other terrestrial radiative forcing terms such as energy and water budgets are also likely. While well-supported by the literature, data, and sensitivity analysis (Figure 2), the trends in Figure (4) represent hypotheses to be tested by the next-generation of observational platforms, both terrestrial and space-borne. Forest management must ultimately confront the elevated mortality and uncertainty in recruitment and growth when considering options for sustaining forest benefits to society into the future.

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Box 1 Vegetation dynamics definitions

We focus on three main plant demographic processes: recruitment, growth, and mortality. Recruitment (including reproduction) results in the seedling and sapling composition of a plant community following disturbance (156). Growth from sapling to mature plants results in development of mature forests and includes competitive processes. Mortality is a key rate controlling carbon storage and species composition in a plant community and is a dominant demographic rate during a pulse-disturbance (157,158).

Abiotic drivers. Physical factors that cause changes in demography and that respond to global change or to disturbances, such as light, CO_2, soil moisture, humidity, temperature, etc.

Biotic drivers. Biological factors that may drive changes in demography, such as pathogens, insects, herbivores, or competition with other individuals.

Chronic environmental change. Persistently changing drivers of demographic rates. These drivers have a non-stable and directional trajectory, such as rising CO_2, temperature, and *VPD*.

Demographic rate. Any individual-, population-, or community-level parameter that affects the age- and/or size-structure of a population or community, including rates of recruitment, growth, and death.

Demographic driver. An abiotic or biotic factor that, when undergoing a change itself, also leads to a change(s) in one or more demographic rates.

Disturbance. The destruction of live plant biomass in a discrete event (159,160).

Disturbance regimes. Spatial and temporal characteristics of disturbances in a landscape over a long time period, including frequency, return interval, duration, intensity, severity, and size.

Growth. The rate of biomass production over time at the individual or ecosystem scale (i.e. Net Primary Production grams C m^{-2} yr^{-1}).

Land-use and land-cover change. Anthropogenic shifts in forms of cultivation or in vegetation cover such as due to forestry, or conversion of woodlands to crop ecosystems.

Mortality. Defined herein as the complete loss of a plants' ability to reproduce and ultimately loss of cellular metabolism.

Recruitment. The rates of transition of plants from one size class into another (typically in units of individuals m^{-2} yr^{-1}). Recruitment results from the birth and growth of individuals. Herein we consider recruitment from the stage of seed dispersal through seedling growth into the sapling stage.

Self-thinning. Reduction in the number of live plants within a stand, occurring via competition for resources.

Vegetation dynamics. The net outcome of the interplay between disturbances and vegetation demographic rates.

Figures

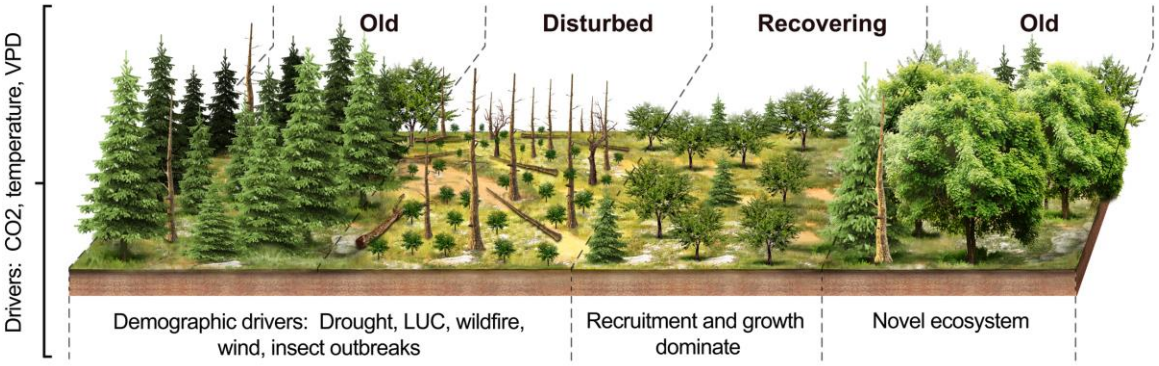


Figure 1. **A conceptual diagram of the components of forest dynamics and disturbances that drive them.** In the far-left panel, a mature ecosystem is responsive primarily to localized mortality, and the primary drivers of demography are chronically changing variables such as CO_2, temperature, and *VPD*. The system is disturbed in the second panel, due to fire, insect outbreak, or another large-scale perturbation that removes much of the overstory trees, and species adapted to rapid post-disturbance recruitment become established. In the third panel recruitment and growth dominate demographic processes, with mortality increasing over time as competition leads to self-thinning. In the last panel, a mature ecosystem is dominated by species that have replaced the original community in response to chronic environmental changes, leading to a novel ecosystem.

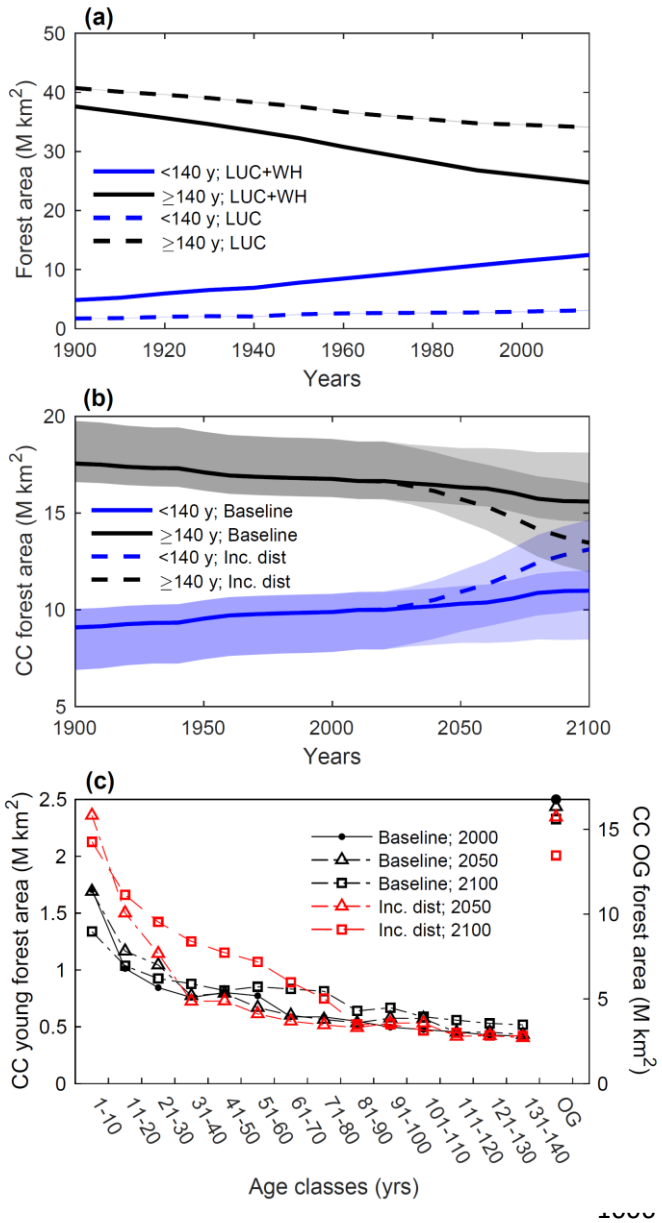
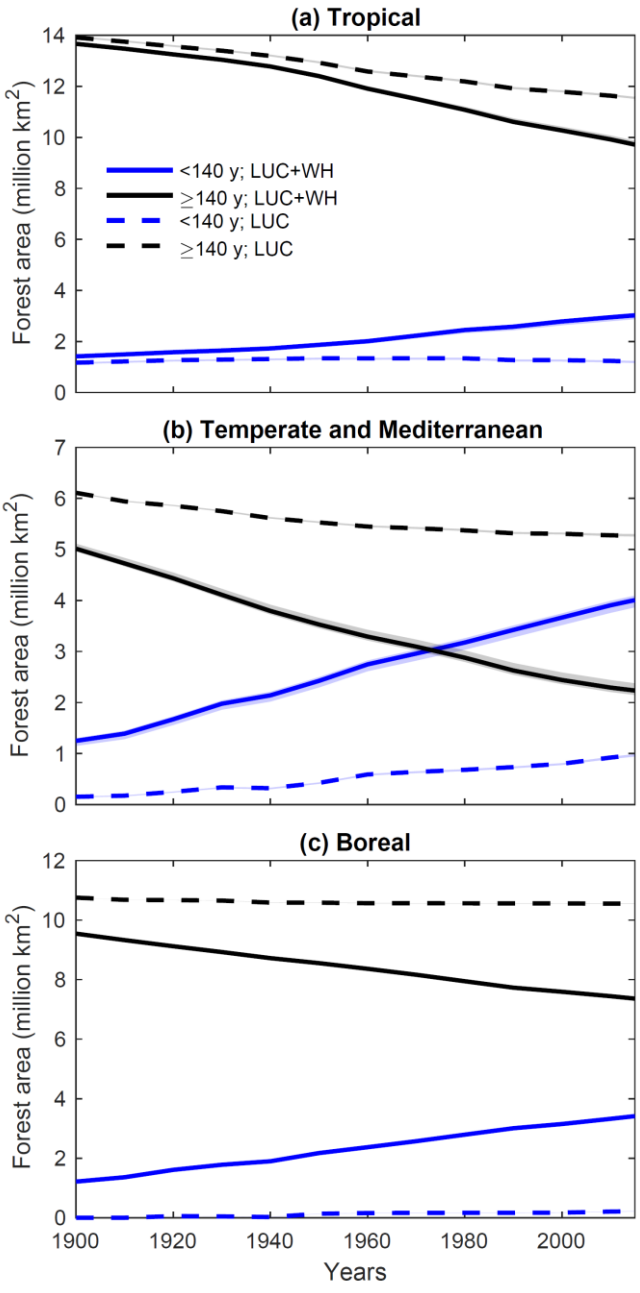


Figure 2. (a) Human activities have increased the amount of young forest area (stands < 140 years old) over the 20th century as a result of both land-use change (*LUC*) and wood harvest (*WH*). Forest stand age distribution was reconstructed using forest-cover transitions from *LUHv2*, initialized using forest cover fractions in 1750 and incrementing forest cover each year, tracking the age of forest up to 140 years. Solid lines show the effect of *LUC* and *WH*, dashed lines *LUC* alone. Total forest area is based on *LUHv2*. The nominal minimum size of a stand is assumed to be *ca.* 0.1 ha. **(b) Sensitivity of age distribution in closed-canopy (CC) forests to plausible changes in disturbance rate.** Forest stand age distribution was reconstructed using forest cover transitions due to *LUC* from *LUHv2* alongside non-*LUC* observation-based disturbance rates (25). In the *baseline* scenario (solid lines), non-*LUC* disturbance is assumed constant at observed 2001-2014 values throughout. In the *Inc. dist* scenario (dashed lines), disturbance rates are incremented linearly to 200% of the 2001-2014 values over the period 2015 to 2050 and held constant at that level thereafter. The underlying *LUC* scenario is GCAM RCP 3.4 that includes land-based mitigation for CO_2 emissions. Results are presented for closed-canopy forests only (25), which is why total forest area is lower between (a) and (b), as non-*LUC* disturbance rate information is not currently available for open-canopy forests. The shaded areas in panels **a** and **b** indicate the effect of assuming that disturbances are five times more likely to affect the youngest forests versus old-growth, or vice versa, as opposed to an even probability across ages (solid lines). The apparent large dampening of this assumption in **a** vs **b** is primarily due to the different y-scales. **(c) Changes in the disturbance regime propagate through forest age structure at decadal time scales.** Closed-canopy young (<140 years old) forest area is shown on the left-hand y-axis. Old-growth (>140 years old; OG) forest area is shown on the right axis (same units) and refers to the data points in the upper right-hand of the panel. Scripts used and additional methods can be accessed at https://github.com/pughtam/AgeClassReconst_rel.git.

1017 Figure 3. **Human activities have increased the amount of young forest area irrespective of biome.**
1018 As for Figure 2a, but broken down by biome[161].

1019



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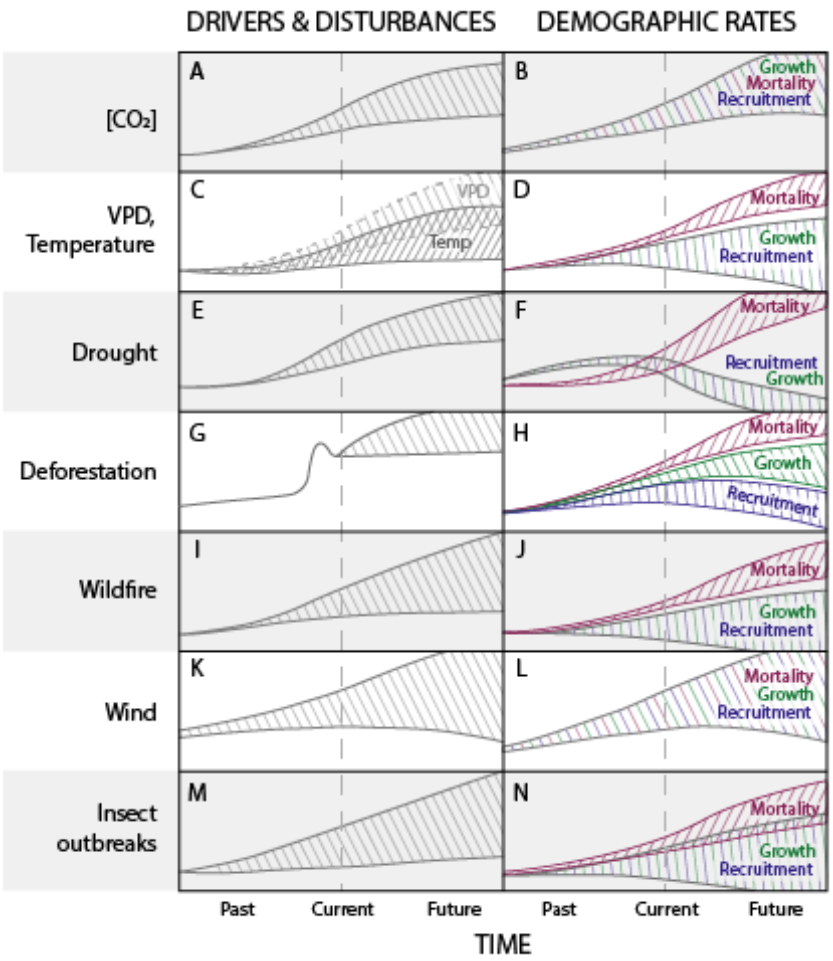

Figure 4. Drivers, disturbances, and demographics are changing both historically and into the future. A graphical summary of the literature evidence of changing drivers and disturbances (left-hand column) and subsequent demographic rates (right-hand column). Shown are the chronically changing drivers A) CO_2, C) *VPD* and temperature and the more transient disturbances of E) drought (low precipitation), G) deforestation, I) wildfire, K) wind, and M) insect outbreaks. Each driver or disturbances' corresponding demographic responses (shown as carbon fluxes per area^{-1} time^{-1}) are shown on the right-hand panels.

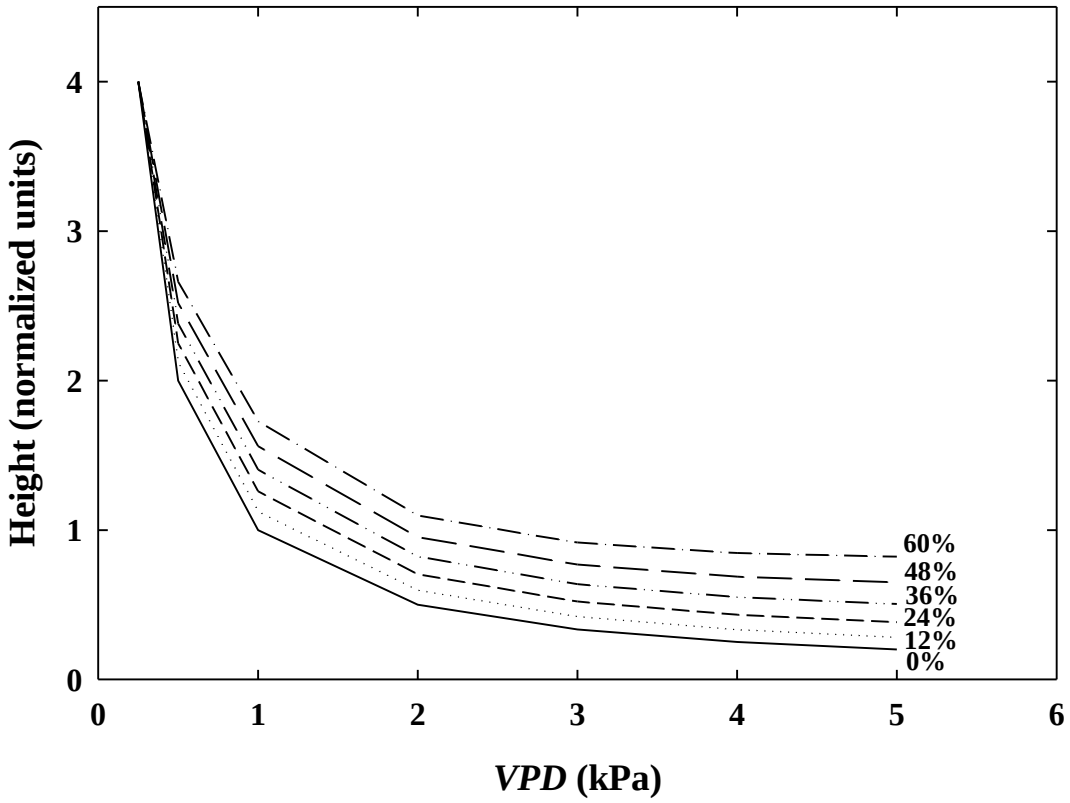

Figure 5. Rising *VPD* forces declines in potential plant stature. Predictions of plant height in response to rising *VPD* from the hydraulic corollary to Darcy's law. The equation is $h = A_s*k_s*(\Delta\Psi)/G*A_l*VPD$, where h is height, A_s is sapwood area, k_s is specific conductivity, $\Delta\Psi$ is the leaf to soil water potential gradient, G is stomatal conductance, and A_l is leaf area[53]. The different lines represent different levels of acclimation of A_s, k_s, $\Delta\Psi$, G, and A_l, all allowed to adjust simultaneously from 0 to 60% from their initial values. In the case of G it is assumed to decrease due to rising atmospheric CO_2. Acclimation can help, but not completely mitigate, the impacts of rising *VPD* on plant size.